THE EPIPHYSEAL COMPLEX IN TRACHYSAURUS RUGOSUS

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INTRODUCTION

Gladstone and Wakeley (1940), quoting earlier workers (Spencer 1886 and Legge 1897), describe the epiphyseal complex of two skinks, *Cyclodus gigas* and *Gengylus ocellatus*. In these lizards the parietal eye appears to be a degenerate structure. *Cyclodus gigas* has a long, well-developed pineal organ, and a parietal foramen, but no parietal eye. In *Gengylus ocellatus*, a parietal eye was found in the embryo only; in the adult there was a large pineal organ, but again no parietal eye. A drawing of the parietal eye of *Scincus officinalis*, from Calvet (1934), is reprinted; the nerve, lens, and retina seem well developed, but the epidermal scale covering the eye is densely pigmented and quite opaque. Gladstone and Wakeley therefore conclude that in the Scincidae, the parietal eye is atrophied and purely vestigial.

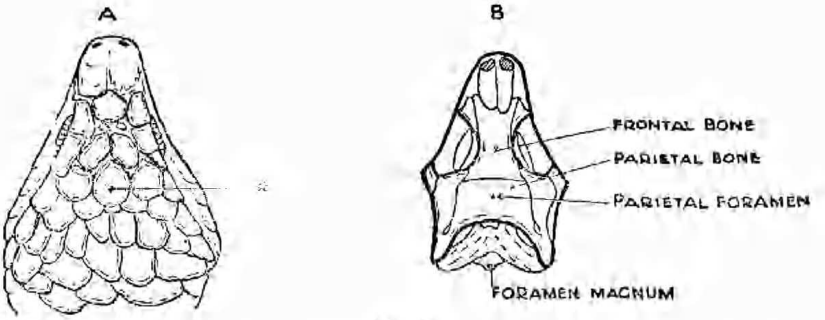

Fig. 1

A. Dorsal aspect of head of *Trachysaurus rugosus* showing parietal fleck and foramen (× ½).
B. Dorsal aspect of skull showing parietal foramen (× ½).

The epiphyseal complex in its fullest development, as seen in *Sphenodon*, comprises the following structures:

I. The pineal organ proper, a sac-like ependymal diverticulum, with an enlarged end-vesicle probably representing an eye which has failed to emerge from the cranial cavity. The organ sends nerve fibres to the habenular ganglia (right nucleus in *Sphenodon*).

II. The parietal eye, a simple vesicular organ lying in the parietal foramen. It shows:

(i) a retina of three layers: an inner layer of cylindrical neurosensory cells, a middle of plexiform nerve fibres, and an outer layer of ganglion cells;
(ii) a lens, of translucent columnar cells;
(iii) a parietal nerve, ending in the left habenular ganglion in *Sphenodon*, but in the right in the Lacertilia.

The parietal eye lies anterior to the pineal organ; it is suggested that in the earliest vertebrates, both lay side by side as dorsal paired eyes (Dendy, 1911).

It is of some interest, therefore, to find that all these structures noted in *Sphenodon* can be found in the skink *Trachysaurus rugosus*. Moreover, they are quite as well differentiated.

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MATERIAL AND METHODS

The material comprised four adult lizards, and one 60 mm. foetus. These were investigated by gross dissection, and also microscopically. Both transverse and longitudinal sections were employed and they were stained with haematoxylin and eosin, picro-indigo-carmine, Weigert-Pal, or De Castro's silver stain, according to requirements.

FINDINGS

1. The dorsum of the skull shows a *parietal foramen,* less than ½ mm. in diameter on the surface, but expanding to a cup-like recess on the inner aspect (fig. 1).

2. In the *parietal scale* over this foramen there is a depression, in some lizards markedly paler than in the rest of the scale. E. R. Waite's (1929) description of the "pineal area" as a group of nine small scales may prove a little misleading, since the actual scale covering the parietal eye is single, constant and relatively large.

3. Sagittal sections show a *parietal eye,* a vesicle of columnar cells lying in the inner part of the foramen, in loose and extremely vascular connective tissue (fig.2). The vesicle shows regional differentiation. The superior quadrant consists mainly of very tall columnar cells, with a few interspersed sphenoidal cells not attached to either basement membrane. This arrangement provides a biconvex lens entirely free from pigment. The remainder of the vesicle forms a retina, sharply defined from the lens and heavily pigmented. Three rather indistinct layers, comparable with those described in *Sphenodon,* can be identified: an inner, of heavily pigmented columnar cells, sending irregular processes towards the centre of the eye; a middle of tangential fibres, and an ill-defined outer layer of ganglion cells, with strands of pigment. The hyaline external limiting membrane is very well developed. Whether the black pigment of the retina was intracellular could not be determined. Some debris in the centre of the vesicle may represent a vitreous body.

The epidermis over the foramen is less pigmented than elsewhere (in the section, fig. 2, the epidermis has slipped to the left where the unpigmented area is clearly visible at *). The connective tissue filling the foramen between eye and skin is devoid of pigment. This tissue has a strongly lamellar structure in fixed material and seems comparable with the more massive parietal plug seen in *Sphenodon.*

Connective tissue immediately around the eye is condensed to form an ill-defined capsule and in the region of the foramen contains many melanophores.

In the foetal specimen, the eye is represented by only a simple diverticulum from the roof of the third ventricle, extending up to the parietal region (fig. 4).

4. The *pineal organ* proper, as distinct from the parietal eye, lies more posteriorly. It is a twisted cylindrical diverticulum, arising from the caudal end of the roof of the third ventricle. The cells are apparently ependymal, being clear and columnar, and they rest on a very clear basement membrane (fig. 3*).

The sac is continuous with a spherical terminal vesicle, very closely resembling the parietal eye; there is even a lens-like thickening of the superior wall. However, the rest of the vesicle is almost devoid of pigment and, unlike the parietal eye, contains no true ganglion cells. There is no gap in the skull over this pineal vesicle.

The stalk of the pineal sac is related anteriorly to the dorsal sac, which reaches almost to the terminal vesicle; it is a thin walled diverticulum, adherent in its turn to the paraphysis. The paraphysis is lined with cuboidal cells and is in continuity with the choroidal plexus of the lateral ventricles. In the foetal specimen the paraphysis was extremely well developed.

5. The *nervous connections* were not satisfactorily established. A nerve was seen to leave the parietal eye from its postero-ventral quadrant, but could not be traced to the habenular region, where presumably it arose. No nerves attached to the pineal sac could be found.

The epithalamic structures, habenular nuclei and commissures are, however, well developed, with a large median habenular nucleus. Nerve fibres ascend from these nuclei in the direction of the parietal eye; but their destination could not be determined.

The whole complex is embedded in a loose connective tissue which is enclosed within a tubular meningeal sheath (fig. 5).

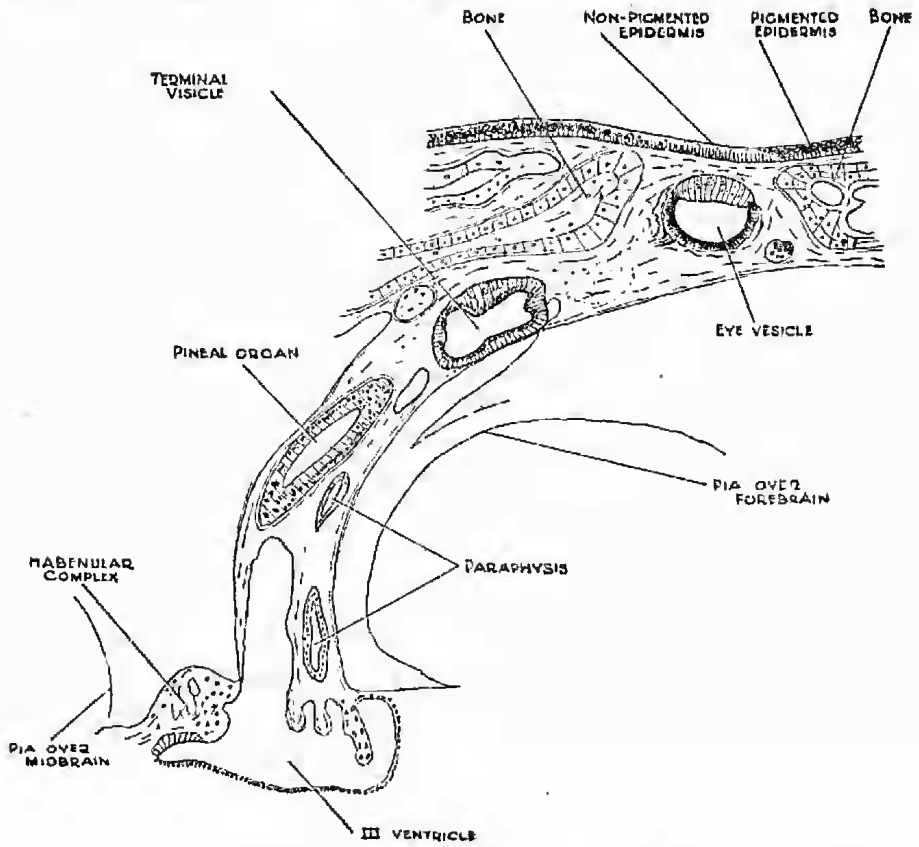

Fig. 5

Composite figure to illustrate most of the features of the epiphyseal complex (x 25 approx.).

DISCUSSION

Trachysaurus rugosus has thus a well-developed parietal eye, with no obvious signs of degeneration, and at least the equal of that in *Sphenodon*. Like other vertebrate parietal eyes, it is very primitive, with no equipment for focussing.

It has been much disputed whether the pineal sac and the parietal eye are developed from two bilateral eyes—later becoming median (Dendy, 1911), or

from primarily median diverticula (Tilney and Warren, 1919). Both theories are equally compatible with the observations made in *Trachysaurus,* and this investigation does nothing to settle the controversy.

It is impossible in a discussion of form to avoid speculation on function. Anatomically, the parietal eye of these lizards seems well adapted to act as a simple light receptor, though most writers deny such function in living reptiles. The pineal sac may conceivably have a glandular function; the paraphysis is so evidently part of the choroidal system that it may be presumed to secrete cerebro-spinal fluid.

No physiological proof of a pineal glandular activity in reptiles is available; the only real evidence for a photo-receptive function comes from the work of Clausen and Mofshin (1939). These authors studied the oxygen consumption of lizards (*Anolis carolinensis*) in the light and in the dark, before and after pinealectomy, and found that pineal "vision" makes a significant difference.

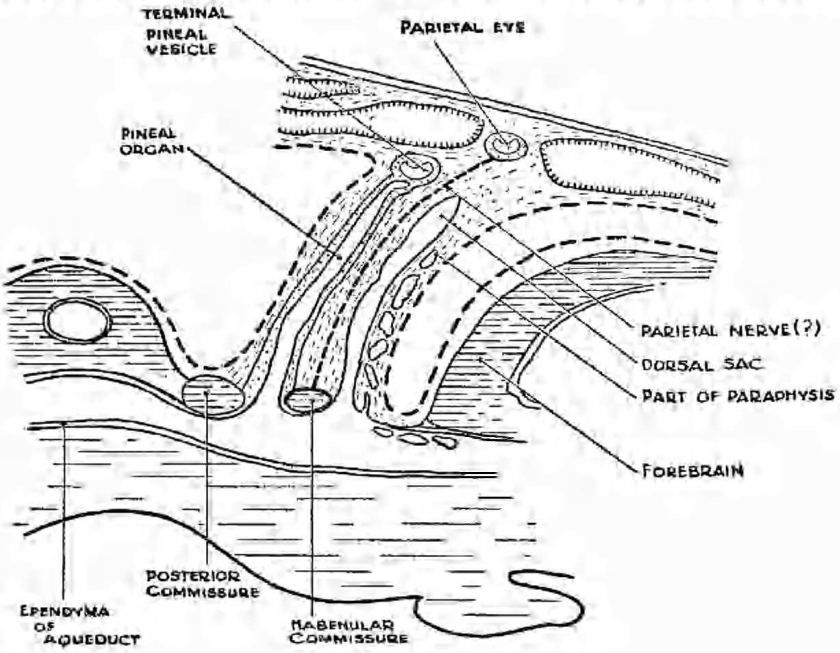

Fig. 6

Diagrammatic reconstruction of the epiphyseal complex.

The course of the parietal nerve and the relations of the dorsal sac and paraphysis are partly hypothetical. (Not drawn to scale.)

From an anatomical view, one may say for *Trachysaurus* what Dendy (1911) said for *Sphenodon*:

"I think we must admit that the pineal eye of *Sphenodon* is no longer at the summit of its career as a light percipient organ, but the evidences of degeneration are very slight. . . . It is impossible for me to believe that an organ which retains such a complex histological structure . . . can be entirely functionless."

ACKNOWLEDGMENTS

I am indebted to Professor A. A. Abbie, who first came upon this eye during an operation and suggested it as a subject for investigation; he has also assisted me with advice throughout this work. Dr. Adey has helped me with the micro-photographs of sections kindly prepared by Mr. T. Canny. Miss G. Walsh was good enough to make the drawings from my draft sketches. I wish to express my gratitude for all this assistance.

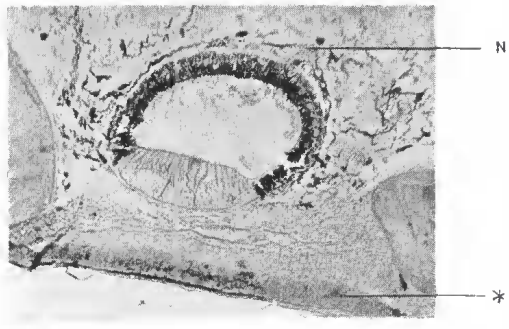

Fig. 2

Photomicrograph of parietal eye. Note overlying parietal foramen, pigmentation in retina and commencement of nerve (N). Haematoxylin and eosin, x 55.

N.B.—During preparation of this section unpigmented epidermis over parietal foramen has slipped to the left (*).

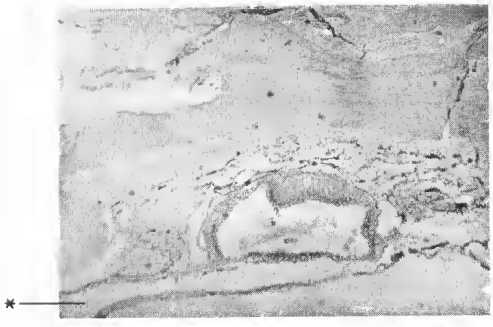

Fig. 3

"Pseudoparietal eye" or terminal vesicle of pineal organ (H. and E., x 32).

Note:

(a) eye-like structure except for pigmentation and nervous connexion;

(b) attached, saccular, pineal organ (*).

(c) that the magnification is less than in fig. 2 in order to show the absence of a foramen in the overlying bone.

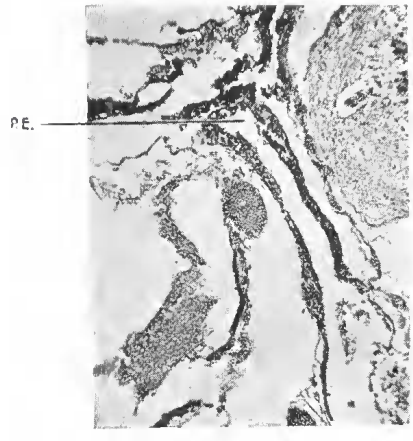

Fig. 4

Sagittal section of the region in a 60 mm. foetus to show the dorsal diverticulum from the root of the third ventricle from the terminal portion of which the parietal eye (P.E.) appears to differentiate (H. & E., x 52).